REPRODUCTIVE BEHAVIOR IN THE SPIDER CRAB, LIBINIA EMARGINATA (L.) [1]

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Crustaceans have complex behavior patterns. Among these are patterns concerned with reproduction and more specifically mating (reviewed by Schöne, 1961). Mating behavior patterns vary among different species and in a number depend upon the physiological condition of the female for their initiation. For example, in some species, mating is correlated with the pre-adult molt of the female and the transferred sperm are stored in the seminal receptacles of the female. Among the portunids, the male protects the pre-molt female and mating occurs immediately after she molts. This behavior is initiated by a pheromone released into the water by the pre-molt female (Ryan, 1966). In some brachyurans (*e.g., Callinectes, Carcinus*), mating is apparently dependent on a condition of ripeness of the ovary (Chidester, 1911; Broekhuysen, 1937). Among Majidae, Schöne (1968) reported that *Maja verrucosa* males protect the females beneath them prior to mating. In some brachyurans submissiveness of the female when seized is necessary for mating to occur (Chidester, 1911). Finally, the mating posture varies among species.

The initiation and probably other aspects of the mating behavior in these crustaceans evidently require rather specific communications between potential mates. In land forms this is often visual and auditory (Salmon and Atsaides, 1968) while in aquatic forms it may also be chemotactic. Chemotatic communication would simply involve one or more pheromones as in the one clear-cut example described by Ryan (1966). In view of the interest in mechanisms of communication in Crustacea as well as other organisms it seemed of interest to report observations on mating behavior of the spider crab, *Libinia emarginata* (L.), and to describe for the first time a heretofore unrecognized male-female association, here called "obstetrical behavior."

Material and Methods

From June to early September, 1967, male and female *Libinia emarginata* obtained from the Marine Biological Laboratory Supply Department, were kept in an aquarium (approximately $3' \times 5' \times 9''$) through which sea water constantly flowed. This arrangement was initially selected to provide storage for the crabs for another purpose. However, as specific behavior patterns began to be recognized, immature animals were removed and only mature animals (5–6 males and 8–14 females) were

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retained. Routine feeding (*Mytilus* and *Spisula*) was initiated, females were marked with insoluble dyes for individual identification, and their brood chambers were examined periodically. The crabs were observed for reproductive behavior at intervals during most of the day and evening.

Observations

Ovigerous females were observed from early June until early September. The females are apparently able to produce at least 3–4 consecutive broods during the period studied. In these crabs spermatozoa enclosed in spermatophores are transferred to the seminal receptacle of the female at mating. At the time of oviposition,

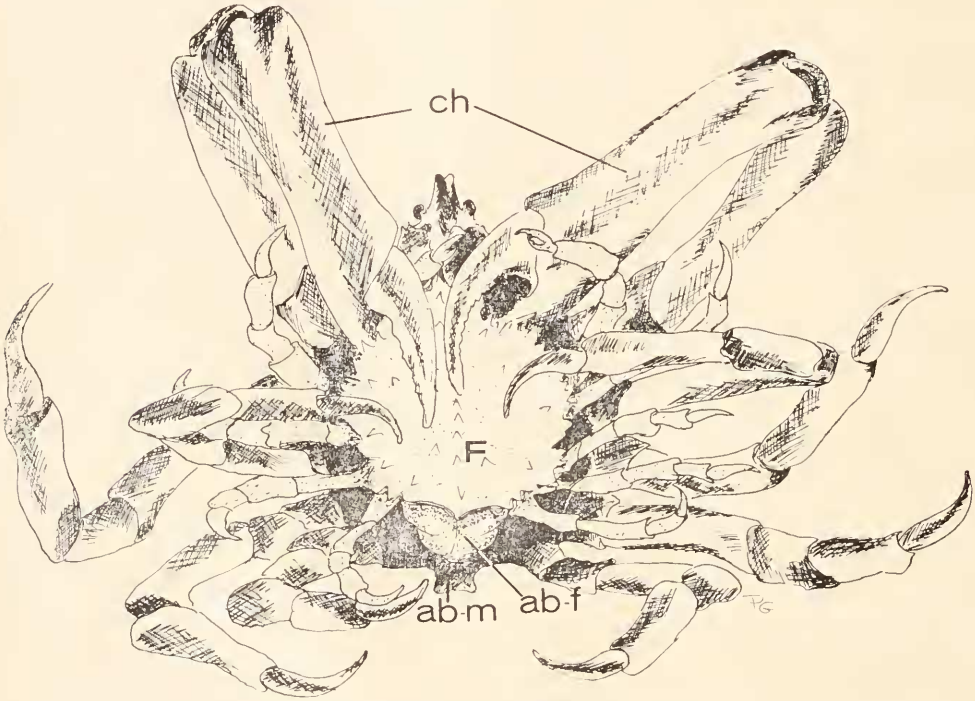

Figure 1. Mating position. Chelae (ch) of the male are bent as he holds the female (F) in the rostral region and rotates onto his carapace. Abdomens of male (ab–m) and female (ab–f) are extended.

the eggs pass the seminal receptacle where they can interact with spermatozoa, and are then discharged into the "brood chamber" where the egg mass becomes attached to the pleopods. The last known date of oviposition in this study was September 1. As has been reported by Costello *et al.* (1957), the eggs at the time of oviposition are a bright orange-red in color. The color changes from orange red to brown as development proceeds in the egg mass. Zoeae were apparent within the egg chorion a few days prior to hatching. In the case of at least six marked females development to the swimming zoea was completed in 25 days. In nine of thirteen

recorded cases, the females had completed oviposition of a new brood in less than 12 hours after releasing zoeae. In four other cases, oviposition occurred after more than 12 hours following zoea release.

Two definite and distinct types of behavior were associated with the release of the zoeae, *i.e.*, mating and obstetrical behavior.

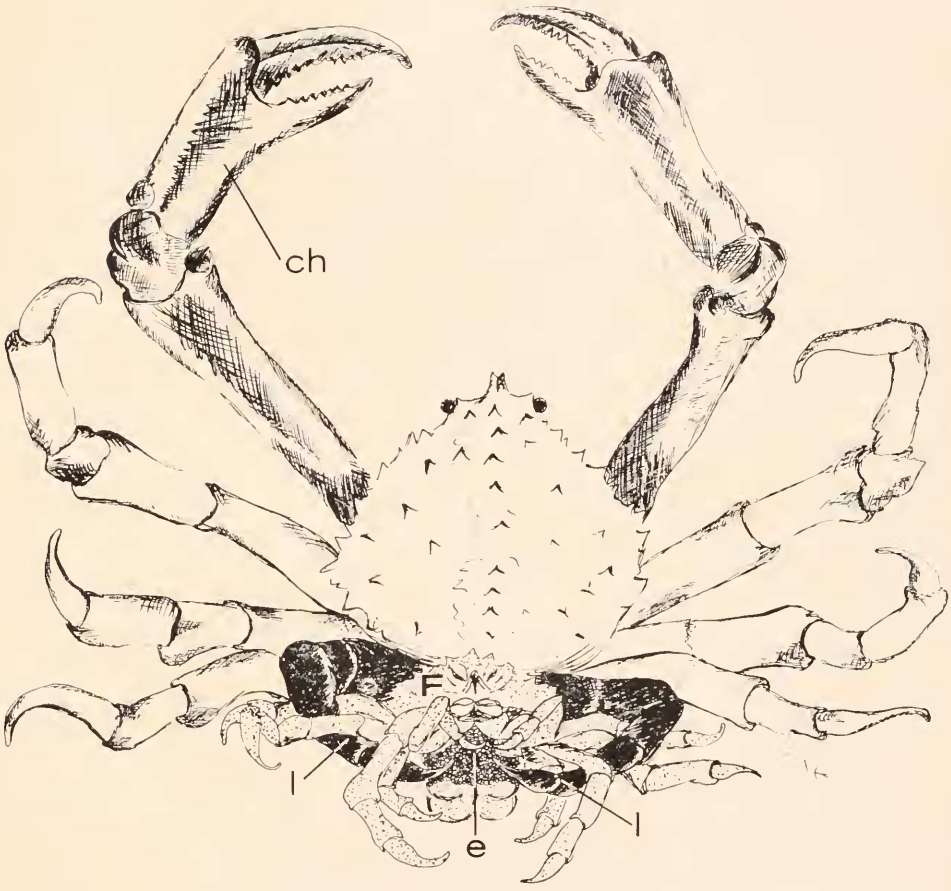

FIGURE 2. Obstetrical position. Female (F) held at right angles to body of the male. The fifth pair of walking legs of the male (l) are inserted into the brood pouch filled with eggs (e) containing zoeae about to hatch. Chelae (ch) of the male are extended at this time.

Mating

In the aquarium containing females about to release zoeae, the males can be observed walking about on the tips of their dactyls. They appear to be actively searching. Encounters at this time with non-gravid females or females which have either just released their larvae or are about to release larvae generally result in mating. Females with eggs in the early stages of development were never observed to mate.

In six recorded cases, the males first grasped the legs of the female with his chelae and positioned her beneath him. His chelae were bent in the manner shown in Figure 1 as he grasped the female in the rostral region. The abdomen of the female was pulled down and bent back at the same time the male's abdomen was lowered. Copulation then began and the male frequently rotated over onto his carapace holding the female above him. Once copulation had been completed, the male resumed a walking position, released his hold on the head of the female, once again grasped her by the legs and released her.

Obstetrical behavior

Immediately preceding the release of zoeae by a female, males were seen actively searching. Males were very aggressive at this time and frequently fought with each other. In sixteen recorded cases, when a female about to release zoeae was encountered, the male captured her and placed her beneath him. Two males might fight for possession of a female and sometimes lose her to a third male. Eventually, a male grasped the female by her legs with his chelae, moved her posteriorly, and positioned her body at right angles to his own. The tips of his fifth walking legs were inserted beneath the abdominal flap to hold her in this position (Fig. 2). The male then frequently backed into a protected area and stood with chelae outstretched. In this position he would fight with other mature males or drive away immature males or females. While being held in this position, the female fanned her abdomen and zoeae were released. Following zoea release she cleaned the remaining egg cases from her pleopods with her chelae. When she had finished the cleaning operation the male released her. Juvenile males and females as well as females with broods at early stages of development were never held in such a position by the male.

Discussion

Libinia emarginata is abundant in coastal waters of the north Atlantic. Bumpus (1898a, b) reported the collection of breeding animals from May through early August while Thompson (1899) collected larvae as late as September 4. Costello *et al.* (1957) stated that development from oviposition to release of larvae takes about one month. In the present study, development was completed in 25 days and the last observed date of oviposition was September 1.

In *Libinia emarginata* there seems to be little sexual display other than the searching walk of the male. Mating position seems similar to that observed in other brachyurans (see review, Schöne, 1961). Although copulation occurs only in newly molted females in many crustaceans, mating in adult *Libinia* occurs between broods and is not associated with molting. Whether the female first mates at the time of the final molt to adulthood is not known. Mating between broods is apparently not needed to produce viable embryos. In *Menippe mercenaria* many broods are produced between intermolts and the sperm are carried over at molting (Cheung, 1968). In *Libinia emarginata* females have been observed to mate with more than one male, suggesting that storage of sperm from several males is possible.

Chemical or mechanical stimuli have been implicated in reproductive behavior

in many arthropods. The presence of a pheromone in the portunids has been established (Ryan, 1966). In *Libinia,* the predictability of the onset of mating and obstetrical behavior, the active searching by the males, the increased fighting among males and the selectivity of the animals to be placed in the obstetrical position suggests that the behavior patterns are initiated by some chemotactic substance, *i.e.,* pheromone(s). Direct experimental evidence for the presence of a pheromone has not yet been obtained. Submissiveness on the part of the female in *Libinia emarginata* may be necessary for mating and for the obstetrical behavior.

Assuming the action of a pheromone(s), it must either come from the female or be released by or with the zoeae at hatching. Production of such a substance and initiation of the behavior patterns seem to be independent of time of day since they occurred at all times of day and night although with greater frequency during the evening hours. In the laboratory situation this could be influenced by artificial conditions such as the fluorescent lighting or crowding. However, predictability, selectivity of participants and the fact that behavioral patterns are not interrupted by feeding or grooming activities suggest that this behavior may occur in nature.

What evolutionary advantages are there in the development of such behavioral patterns? The obstetrical behavior may have evolved to protect the female as the zoeae are being released although females are able to release zoeae without the presence of a male. In *Maja,* the male protects the female beneath him while the zoeae are released, (Schöne, 1968). *Libinia emarginata* males have been observed standing over and protecting females which had only two or three legs. They seemed unable to place such females in the obstetrical position. The distinctiveness of the behavior in *Libinia* may in part be accounted for by the great differences in size between male and female.

Among Majidae, both *Libinia emarginata* and *Maja* have a new egg mass in the brood pouch a short time after zoea release. In *Maja,* the crabs mate prior to zoea release. In *Libinia* it seems possible for a female to produce a new egg mass without mating again although mating frequently occurred either before or after zoea release. Production of a pheromone at this time may insure mating before the next brood. Among Majidae where no further molts occur after the adult stage has been attained, mating at the time of zoea release may insure carryover of sperm from one season to the next.

Summary

1. Data concerning reproductive behavior and development in the spider crab, *Libinia emarginata* (L.) are recorded. Ovigerous females were collected from early June to early September. Females are apparently able to produce at least 3–4 consecutive broods of 25 days development each during a breeding season.

2. Two distinct reproductive behavior patterns are associated with the release of zoea on the 25th day of development, *i.e.,* mating and obstetrical behavior. These male-female associations are stereotyped behaviors. The position of the bodies of the male and female differ in the two behavior patterns.

3. The predictability of onset of these behaviors and the specificity of the patterns suggest their possible initiation by pheromone(s).

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